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MUSHROOM CONSUMPTION (MYCOPHAGY) BY NORTH AMERICAN CERVIDS

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ABSTRACT—Native mushrooms play an important, though often underestimated, role in deer, elk, and caribou diets in North America. Mushrooms are often noted as an unusual or anomalous food in the diets of cervids; yet they often dominate diets in the late summer and fall in forested areas of western North America and throughout the year in the southeastern U.S. Mushrooms are particularly high in protein (16–19%), phosphorus (average 0.75%), and potassium (average 2%). Also, mushroom production is generally greatest in fall. Therefore, they are a highly nutritious food in late season when other native forages may marginally meet basal nutrient requirements of ungulates.

Key words: caribou, cervid, deer, diet, elk, mycophagy, mushroom, nutrition, ruminant.

Wildlife scientists have long recognized that certain highly nutritious, "bonus" foods frequently contribute significantly to animal welfare though their contribution (%) to the diet may be small (e.g., acorns, mushrooms, and mesquite beans). By seeking out these high-quality but generally scarce or ephemeral foods, herbivores can balance nutrients against lower-quality forages that are more abundant. Native mushrooms have often been recorded as a "bonus" food in the diets of deer, elk, and caribou in North America. However, their contribution to cervid nutrition is not commonly understood.

The term "mushroom" refers to the fleshy fruiting body (sporocarp) of many species of fungi. Mushrooms are technically not "plants." They belong to the kingdom Mycetae under the five-kingdom classification system (Whittaker 1969). The primary mushroom-producing fungi are in the group called Basidiomycetes, but many mushrooms eaten by wildlife, including morels, are Ascomycetes. Mushroom production is triggered when species-specific requirements of minimum temperature and moisture conditions are met (Smith and Weber 1980).

Mushroom consumption (mycophagy) has been recorded for many wildlife species in North America. Mushrooms are eaten by ungulates (e.g., deer and elk), small mammals (e.g., squirrels and armadillos), as well as birds, turtles, and insects (Miller and Halls 1969, Fogel and Trappe 1978, Martin 1979). Mushrooms have long been recognized as an important component of small mammal diets (Fogel and Trappe 1978). However, mushrooms are seldom considered a significant component of cervid diets even though they have been anecdotally recorded as a "preferred" food item. Discounting mushrooms as an important dietary component may stem from a misunderstanding of their nutritive value. The purposes of this review are to (1) assess the contribution of mushrooms to cervid diets, (2) summarize the known literature on the nutritive value of mushrooms to ungulates, and (3) assess the implications of mycophagy to habitat selection and nutritional ecology.

CONTRIBUTION OF MUSHROOMS TO DEER, ELK, AND CARIBOU DIETS

Mushroom Consumption by Deer

Many studies have recorded mushrooms in diets of both mule (*Odocoileus hemionus*) and white-tailed (*Odocoileus virginianus*) deer (Table 1). Diet composition estimates range from a trace to a majority of the diet. On the upper limit, 71.2% mushrooms, on a fresh-weight basis, were recorded in fall deer diets in Alabama (Kirkpatrick et al. 1969), 65.8% in August diets in Arizona (Hungerford 1970), and 59.5% in August diets in Montana (Lovaas 1958).

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TABLE 1. Proportion of mushrooms in deer, elk, and caribou diets in North America averaged over season[a].

Species State or Province (Vegetation type)[b]	% of diet Spring	 Summer	 Fall	 Winter	Kind of data[c]	Source[d]
Mule deer (*Odocoileus hemionus*)						
Colorado (spruce/fir/pine forest)	–	0.3	–	–	Obs. (% bites)	31
Montana (spruce/fir/pine forest)	0.0	12.1	0.0	0.0	Rum. (% vol.)	21
Utah (dry mountain meadow)	–	7.0	–	–	Obs. (% mass)	10
Utah (mature conifer forest)	–	15.0	–	–	Obs. (% mass)	10
Utah (stagnated conifer forest)	–	14.0	–	–	Obs. (% mass)	10
Utah (conifer forest/oak woodland)	–	5.4	9.3	–	Obs. (% mass)	4
Arizona (mixed-conifer forest)	–	16.4	–	–	Obs. (% time)	16
California (chaparral-oak woodland)	–	–	–	<1.0	Rum. (% vol.)	20
British Columbia (conifer forest)	0.0	0.0	13.0	4.0	Rum. (% vol.)	8
White-tailed deer (*Odocoileus virginianus*)						
New Brunswick (conifer/deciduous forest)	13.7	6.7	9.1	–	Rum. (% mass)	26
Maine (pine-hemlock forest)	0.0	0.0	45.0	0.0	Obs. (% mass)	9
Pennsylvania (clear-cut forest)	1.6	0.2	0.8	4.5	Obs. (% time)	14
Southeastern U.S. (oak-hickory-pine forest)	2.1	19.8	8.4	6.2	Rum. (% vol.)	12
Southeastern U.S. (mixed-pine forest)	0.4	15.6	8.6	4.9	Rum. (% vol.)	12
Southeastern U.S. (southern evergreen forest)	0.6	16.4	5.4	3.2	Rum. (% vol.)	12
Virginia (eastern deciduous forest)	0.0	40.0	2.5	0.0	Rum. (% vol.)	19
North Carolina (oak-hickory-pine forest)	0.0	10.6	7.0	0.0	Rum. (% vol.)	19
South Carolina (mixed pine forest)	0.2	33.4	2.6	10.7	Rum. (% vol.)	19
Georgia (southern evergreen forest)	0.0	9.7	9.0	13.8	Rum. (% vol.)	19
Florida (southern evergreen forest)	1.4	10.4	26.7	13.2	Rum. (% vol.)	19
Florida (southern evergreen forest)	–	–	–	9.2	Rum. (% vol.)	11
Florida (pine-scrub oak forest)	–	–	–	25.2	Rum. (% vol.)	11
Alabama (southern pine-hardwood forest)	0.0	71.2	0.5	17.4	Rum. (% vol.)	19
Alabama (southern pine-hardwood forest)	7.3	–	4.8	0.8	Rum. (% vol.)	1
Louisiana (pine-bluestem range)	0.5	1.5	3.5	<0.5	Obs. (% bites)	28
Louisiana (pine-hardwood forest)	–	0.4	1.9	0.7	Obs. (% bites)	29
Louisiana (clear-cut forest)	–	<0.1	2.1	0.2	Obs. (% bites)	29
Texas (pine-mixed hardwood forest)	3.0	34.0	1.0	7.0	Rum. (% mass)	25
Oklahoma (oak savannah)	0.0	0.0	4.3	1.0	Rum. (rel. freq.)	30
Wisconsin (northern hardwood forest)	–	2.0	–	–	Rum. (% vol.)	22
Minnesota (northern hardwood forest)	–	–	<1.0	0.0	Rum. (% vol.)	2
South Dakota (pine forest)	0.0	4.0	2.1	0.0	Rum. (% vol.)	15
South Dakota (pine forest)	–	0.7	0.5	<0.5	Rum. (% vol.)	23
Elk (*Cervus elaphus*)						
Virginia (eastern deciduous forest)	–	–	1.0	–	Rum. (% vol.)	3
Saskatchewan (pine forest)	–	5.3	–	–	Rum. (% mass)	17
Saskatchewan (mixed forest)	–	4.2	–	–	Rum. (% mass)	17
Utah (dry mountain meadow)	–	4.2	8.3	–	Obs. (% mass)	7
Utah (mature conifer forest)	–	18.7	55.7	–	Obs. (% mass)	7
Utah (stagnated forest)	–	18.4	55.4	–	Obs. (% mass)	7
California (Pacific rain forest)	–	–	0.3	–	Obs. (% time)	13
Caribou (*Rangifer tarandus*)						
Newfoundland (conifer forest)	0.0	25.0	12.0	0.0	Rum. (% vol.)	5
Northern Canada (conifer forest)	–	–	–	0.4	Rum. (% vol.)	24
Northern Canada (boreal forest)	–	1.2	–	–	Rum. (% vol.)	18
Alaska (spruce forest/tundra)	0.0	12.0	10.0	2.0	Obs. (% vol.)	6
Alaska (spruce forest)	–	–	45.0	–	Rum (% vol.)	27

[a] A dash [illegible] % in diet means no data were available.
[b] General descriptions given by authors or vegetation area according to Aldrich 1963.
[c] Obs. = [illegible] data, Rum. = rumen contents.
[d] Key to [illegible]: (1) Adams 1959, (2) Aldous and Smith 1938, (3) Baldwin and Patton 1938, (4) Beale and Darby 1991, (5) Bergerud 1972, (6) Boertje 1984; (7) Collins 1977, (8) [illegible] 1945, (9) Crawford 1982, (10) Deschamp et al. 1979, (11) Harlow 1961, (12) Harlow and Hooper 1971, (13) Harper 1962; (14) Healy 1971, (15) Hill and [illegible], (16) Hungerford 1970, (17) Hunt 1979, (18) Kelsall 1968, (19) Kirkpatrick et al. 1969, (20) Leopold et al. 1951, (21) Lovaas 1958, (22) McCaffery et al. 1974, (23) [illegible] 1972, (24) Scotter 1967, (25) Short 1971, (26) Skinner and Telfer 1974, (27) Skoog 1968, (28) Thill and Martin 1986, (29) Thill et al. 1990, (30) Van Vreede [illegible], [illegible] et al. 1972.

Late summer and fall are generally the seasons of greatest mushroom consumption, probably because mushroom production is generally greatest then. Though mushroom biomass production is seldom recorded in diet studies, several authors note that mushroom production is triggered by fall rains (Tevis 1952, Hungerford 1970, Urness 1985).

The mushroom species most consumed by deer are not precisely known because species are seldom recorded in diet surveys and preference studies have not been conducted. In addition, species identification is rare because most wildlife researchers are not acquainted with common mushroom species and professional taxonomic help is difficult to obtain (Cowan 1945). In most field studies, mushrooms are categorized into groups such as "field mushrooms," "mixed-mushrooms," or simply "fungi." However, when listed, species of the following genera are consistently taken by deer: *Amanita* (Hungerford 1970), *Armillaria* (Healy 1971, Miller and Halls 1969), *Boletus* (Cowan 1945, Hungerford 1970, Beale and Darby 1991), *Clavaria* (Dixon 1934), *Clitocybe* (Cowan 1945, Beale and Darby 1991), *Cortinarius* (Hungerford 1970), *Morchella* (Cowan 1945), *Lactarius* (Miller and Halls 1969), *Lentinus* (Dixon 1934), *Polyporus* (Skinner and Telfer 1974), *Russula* (Cowan 1945, Miller and Halls 1969, Hungerford 1970), and *Suillus* (Miller and Halls 1969).

Mushroom Consumption by Elk

Elk (*Cervus elaphus*) diet studies rarely record fungi as a component. An extensive literature review of elk food habits in 1973 did not mention mushrooms as a recorded food item (Kufeld 1973). However, at least four studies have recorded mushrooms as a component of elk diets (Table 1). Composition estimates range from a trace to as high as 75% on a dry-weight basis (Collins et al. 1978). As with deer, mushroom consumption is greatest during seasons of greatest availability—late summer and fall.

It seems reasonable to assume that mushroom species sought by deer would also be acceptable to elk, though evidence is lacking. Collins (1977) listed species of *Aleuria*, *Boletus*, and *Russula* as important and "highly preferred" dietary components.

Mushroom Consumption by Caribou

Mushrooms have often been recorded as very palatable and highly sought dietary items in caribou (*Rangifer tarandus*) diets. When mushrooms are available, they may constitute 10–25% of caribou diets, but they may average as much as 45% (Table 1) and have been recorded as high as 84% in one individual (Skoog 1968). Even in winter, reindeer "unerringly" detect snow-covered frozen mushrooms, "consuming them greedily" (Karaev 1968). Boertje (1981) reported that most genera of mushrooms are taken without hesitation by caribou. Mushrooms of the genera *Boletus*, *Coprinus*, *Lactarius*, *Lycoperdon*, *Morchella*, and *Russula* have been listed as major dietary components (Karaev 1968, Skoog 1968, Boertje 1981).

NUTRITIVE VALUE OF MUSHROOMS

Many authors state that deer, elk, and caribou "strongly prefer" mushrooms and in some cases actually travel from site to site seeking mushrooms. The obvious question is, why? What nutritional benefits do cervids gain from fungi? Some authors consider mushrooms nearly devoid of nutrition, while others suggest they compare favorably with soybeans or spinach (Crisan and Sands 1978).

Little is known about the true nutritive value of mushrooms since few comprehensive studies have been conducted. Crisan and Sands (1978) conducted a thorough literature review on the nutritive value of wild mushrooms to monogastrics (e.g., humans). Several range and wildlife scientists have collected and analyzed mushrooms prominent in ruminant diets. But, the nutritional procedures used by most range and wildlife scientists were designed to analyze grasses and forbs. When these procedures are applied to mushrooms, the results are often incorrectly interpreted because mushrooms are much different from vascular plants in their chemical composition. Further information on the nutritive value of mushrooms can be gained from research on mycophagy by insects and small mammals. The following discussion is a summary and interpretation of nutrition studies to assess the value of mushrooms to ruminant animals.

Moisture Content of Mushrooms

Over 80% of the fresh weight of most mushrooms is water (Table 2). This large water proportion requires that the consumer eat large volumes to obtain nutritional benefit, although high water content rarely restricts intake. The

Table 2. Nutritive value and digestibility of wild mushrooms[a].

Composite samples based on:	Initial moisture	Crude protein	Ash	Fat	N-free extract	Fiber	Calcium	Phos-phorus	Digesti-bility	Source[b]
Species available	–	34.8	8.1	4.8	31.6	20.8 (crude)	–	–	–	7
Species available	–	23.0	9.0	5.0	48.0	15.0 (crude)	–	–	–	5
Species available	83.9	21.5	6.6	3.9	54.2	13.8 (crude)	0.09	0.56	–	4
Species in cattle diets (summer)	–	22.0	–	–	–	– –	<0.10	0.42	–	2
Species in cattle diets (fall)	–	25.0	–	–	–	– –	<0.10	0.55	–	2
Species available (winter)	89.4	22.1	–	–	–	– –	0.08	0.46	58.8	1
Species available (spring)	87.6	23.1	–	–	–	– –	0.07	0.47	64.7	1
Species available (summer)	87.2	29.0	–	–	–	– –	0.05	0.53	56.6	1
Species available (fall)	85.9	24.8	–	–	–	– –	0.04	0.53	59.9	1
Species in deer diets	88.9	21.3	–	–	–	– –	–	–	80.8	6
Species in elk diets	89.5	24.1	–		–	– –	–	–	77.5	6
Species in caribou diets (summer)	–	34.7	–		–	31.7 (NDF)	0.03	0.70	90.0	3
Species in caribou diets (fall)	–	35.3	–	–	–	31.5 (NDF)	0.03	0.71	90.0	3
Species in caribou diets (winter)	–	40.0	–	–	–	29.9 (NDF)	0.03	0.79	91.0	3

[a]All data expressed as a % of dry matter except initial moisture, which is expressed as % of fresh weight.
[b]Key to references: (1) Blair et al. 1984, (2) Bjugstad and Dalrymple 1968, (3) Boertje 1981, (4) Crisan and Sands 1978, (5) Kelsall 1968, (6) Pallesen 1979, (7) Syrjala-Qvist 1986.

addition of water to the rumen per se has little effect on intake because it is easily absorbed or removed (Van Soest 1982). Mushrooms may in fact be an important source of water for some mammals (Fogel and Trappe 1978).

Mushrooms as an Energy Source

Mushrooms, like true plants, contain lipids (or fats), nonstructural carbohydrates, and fiber that are all used as energy sources by ruminants. The average gross energy of mushrooms ranges from 300 to 400 kcals per 100 grams dry weight. Fleshy fungal tissue compares favorably with many fruits and vegetables but is less rich in energy than seeds or nuts (Martin 1979).

The fat content of edible mushrooms ranges from <1% to as high as 20% (Crisan and Sands 1978). On average, however, mushrooms contain 2–6% fat. The fat component of fungal tissue includes free fatty acids, mono-, di-, and triglycerides, sterols, sterol esters, and phospholipids.

On a dry-weight basis, mushrooms are primarily composed of nonstructural carbohydrates (nitrogen-free extract [Table 2]). A large variety of compounds make up the carbohydrate components, including pentoses, methyl pentoses, hexoses, disaccharides, amino sugars, sugar alcohols, and sugar acids (Crisan and Sands 1978). By comparison, the most prominent nonstructural carbohydrates in green plants are fructosans, sugars, dextrin, and starch (Trlica 1977).

In plants most energy available to ruminants comes from the microbial degradation of fibrous cell walls. However, fungal cell walls are much different from those of higher plants. The primary component of fungal cell walls is chitin,whereas plant cell walls are mostly cellulose (Crisan and Sands 1978, Martin 1979). Chitin is a N-acetylglucosamine polymer linked with β-1,4 bonds similar to cellulose. Unlike the fiber of higher plants, chitin contains a significant proportion of nonprotein nitrogen as an amino sugar. A β-glucan, with β-1,3 linkages and β-1,6 branches, also forms a part of the cell wall (Martin 1979). Additionally, lignin and pectin are not known to occur in fungi.

Protein Content of Mushrooms

Early investigators used the term "vegetable meat" to describe mushrooms because analysis revealed that native mushrooms contain 20–50% of their dry matter as protein (Peck 1895). More recent studies on mushroom protein content suggest that mushrooms probably rarely reach 50% protein by dry weight. However, relatively speaking, mushrooms are an excellent protein source. There is extreme variation in protein content from a low of about 4% to as high as 44% depending on species, stage of growth, and environmental conditions (Crisan and Sands 1978). By comparison, fresh-cut alfalfa (*Medicago sativa*) is generally 16–19% protein (Jurgens 1978).

Crude protein is usually calculated by multiplying total nitrogen, determined by Kjeldahl analysis, by 6.25. This correction factor is based on the assumptions that most proteins contain 16% nitrogen, that these proteins are completely digestible, and that amounts of nonprotein nitrogen in the cell are negligible. Since a substantial amount of nitrogen in mushrooms is in chitin and other nonprotein compounds, such as urea and nucleic acids, Crisan and Sands (1978) suggested a correction term based on the assumption that only 70% of the nitrogen in mushrooms is in the form of digestible protein (70% N * 6.25 = 4.38). This correction term of 4.38% may be conservative when considering the use of mushrooms by ruminants and comparing mushrooms to other forage eaten by ruminants. Only 60–70% of the nitrogen in fungal tissue is in the form of protein (Moore-Landecker 1982). However, this estimate is similar to the proportion of nitrogen in proteins in forage plants (60–80%; Van Soest 1982). Furthermore, nonprotein nitrogen, such as urea, is readily converted to ammonia by rumen microbes and is either used for microbial growth or absorbed across the rumen wall. The nitrogen fraction of chitin is unavailable to monogastrics but is probably converted to microbial protein in the rumen. In fact, chitinous nitrogen may be more available to ruminants than the cell-wall nitrogen of higher plants due to the lack of lignin in fungi.

Vitamin and Mineral Composition of Mushrooms

Mushrooms are a good source of several vitamins including the B complex and vitamin C (Change 1980, Crisan and Sands 1978). However, these are not essential vitamins for ruminants because they can be synthesized by rumen microbes (Van Soest 1982). Additionally, mushrooms are basically devoid of vitamins A and D, which are essential dietary components for ruminants.

Mushrooms accumulate minerals from the soil and plant material on which they grow. Therefore, mushrooms probably contain all the minerals present in their growth substrate (Crisan and Sands 1978). Stating average mineral concentrations may be misleading because mineral concentration varies greatly depending on species and soil fertility. For example, though potassium level averages 2% (in 24 species from several locations), it varies from 0.18 to 4.8% (Crisan and Sands 1978).

The most abundant minerals in mushrooms are potassium, averaging about 2% dry weight, and phosphorus, averaging about 0.75% (Change 1980, Crisan and Sands 1978, Martin 1979). Both mineral levels exceed maintenance requirements of most weaned ungulates (based on sheep and cattle requirements; Jurgens 1978). Mushrooms also contain calcium but at lower concentration than phosphorus or potassium. However, calcium concentration averages 0.14%, which would not meet calcium requirements of weaned deer (Ullrey et al. 1973). Calcium is often in excess of ruminant needs in other forages, while phosphorus is more commonly inadequate.

Digestibility of Mushrooms

The degradation of fungal cell walls requires chitinase and β-1,3 and β-1,6 glucanases (Martin 1979). Chitin is degradable in the rumen because of chitinase activity by rumen microbes, although there may be an adaptation period necessary to obtain adequate levels of chitinase activity (Cheeke 1991). The ability of rumen microbes to degrade the β-glucans in fungal cell walls is unknown.

The in vitro digestibility of mushrooms is very high relative to other ungulate forages (Table 2) and may exceed 90% in some cases. Consequently, identification of mushrooms in fecal analysis is rare (Boertje 1981).

IMPLICATIONS OF MYCOPHAGY BY DEER AND ELK

To conclude this discussion it is fair to ask, What difference does it make if deer, elk, or caribou eat mushrooms or not? Mycophagy by cervids may be important for several reasons. First, mushrooms undoubtedly make an important, though sporadic, contribution to cervid nutrition in mushroom-rich environments. Mushrooms are highly preferred and nutritious foods for cervids, particularly in late summer and fall in forested areas of western North America and throughout the year in the Southeast. Mushrooms may be a particularly important protein and phosphorus source in late season when many forages yield only enough digestible dry matter to meet basal energy requirements (Short 1975, Blair et al. 1984). Therefore, even a few bites of mushrooms by an herbivore may contribute substantially to meeting the nutritional requirements and helping to balance nutrients obtained from other forages of quite different composition.

Second, mushrooms may attract herbivores to mature and stagnated forest areas that might otherwise go unused as foraging areas (Rasmussen 1941, Collins et al. 1978, Warren and Mysterud 1991). Additionally, mushrooms may become an important dietary supplement when herbivores are forced to seek densely forested areas for protection from biting insects or predators (Bergerud 1972). Mushroom production is usually greatest in dense forested areas, in part because mushrooms do not require sunlight for growth.

Finally, fungi play an important symbiotic role in mycorrhizal relationships with several conifer species, including ponderosa pine (Kotter 1984). Since the spores of fungi are apparently not destroyed in the rumen, herbivores may serve as vectors for fungal spores to initiate mycorrhizal associations (Fogel and Trappe 1978).

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